

THE PEA CRAB *ORTHOOTHERES HALIOTIDIS* NEW SPECIES (DECAPODA: BRACHYURA: PINNOTHERIDAE) IN THE AUSTRALIAN ABALONE *HALIOTIS ASININA* LINNAEUS, 1758 AND *HALIOTIS SQUAMATA* REEVE, 1846 (GASTROPODA: VETIGASTROPODA: HALIOTIDAE)

Daniel L. Geiger and Joel W. Martin

ABSTRACT

A new species of pinnotherid crab, *Orthotheres haliotidis*, is described from two species of Australian abalone, *Haliotis asinina* Linnaeus, 1758, and *H. squamata* Reeve, 1846. Its morphology is recorded using light and scanning electron microscopy. The report is the second record of the predominantly American genus *Orthotheres* in the western Pacific, the first confirmed record of a pinnotherid crab from any species of abalone, and the first record of a pinnotherid associated with *H. squamata*.

Commensalism between pea crabs (Brachyura: Pinnotheridae) and various invertebrates are fairly well known and documented; Schmitt et al. (1973) listed as hosts 10 phyla from Cnidaria to Chordata: Ascidia. Pea crabs have been found within the Mollusca, in one chiton, 19 prosobranchs (Table 1), four opisthobranchs and in 182 bivalves. Since then a number of additional associations between pea crabs and mollusks have been described notably most with bivalves (Bhavanarayana and Devi, 1974; Fischer and Fischer-Piette; 1976, Konishi, 1977; Stevens, 1992; Zmarzly, 1992; Campos, 1993; Schneider, 1993; Korkos and Singer, 1995), however, only one with a further gastropod host (Campos, 1989: table 1).

In abalone only a few commensals are known. The association between the alpheid shrimp *Betaeus harfordi* (Kingsley, 1878) with all six California abalone species has been described (Cox, 1962; Chace and Abbott, 1980; Jensen, 1995). Pinnotherid crabs have been indicated from two abalone species: *Haliotis asinina* Linnaeus, 1758, and *H. coccoradiata* Reeve, 1846 (Haswell, 1882, Grant and McCulloch, 1906, Allen, 1959, Fischer, 1976). The identification of that symbiont as *Pinnixa faba* (Dana, 1851) is problematic as already pointed out by Rathbun (1918) and Schmitt et al. (1973). *Pinnixa faba* is restricted to the northeastern Pacific, and is usually associated with bivalves (see Schmitt et al., 1973). The abalone host species, however, are restricted to the tropical Pacific (*H. asinina*) and Australia (*H. coccoradiata*). No material was ever deposited for which reason the identity of the symbiont could not be verified. We suspect those records are based on misidentification of the new species we describe below. We base our discussion on two specimens of *Haliotis* (*H. asinina*, *H. squamata* Reeve, 1846: fig. 1), each of which contained one pair of pea crabs.

The pinnotherid genus *Orthotheres* Sakai, 1969, contains five species (see revision by Campos, 1989): *O. turboe* Sakai, 1969 (type species by original designation), *O. barbatus* (Desbonne, 1867), *O. serrei* (Rathbun, 1909), and *O. strombi* (Rathbun, 1905), and *O. unguifalcula* (Glassell, 1936). All species in the genus have been reported from gastropod hosts (*Turbo*, *Cittarium*, *Strombus*, *Pleuroplaca*) with the exception of *O. unguifalcula*, which may have been associated with a starfish, although this needs confirmation (Campos, 1989). Three of the five species (*O. barbatus*, *O. serrei*, *O. barbatus*) are known only

Table 1. Prosobranch host and pinnotherid commensal. From Schmitt et al. (1973), Fischer (1976), Campos (1989), Mannig and Holthuis (1981), Manning (1993), this study. 1: Identification doubtful fide Schmitt et al. (1973). 2: As *Conus papilloaceus* Hwass, synonymy according to Abbott and Dance (1983) and Bernard (1984). 3: Generic reassignment according to Campos (1989). 4: Generic reassignment according to Campos (1990). 5: May also be assigned to *Calyptraeotheres* (Campos, 1990). 6: Generic assignment questionable (Campos, 1990: 369). 7: Generic reassignment according to Manning (1993).

Gastropod Host	Symbiotic Pea Crab
Haliotidae	
<i>Haliotis asinina</i> Linnaeus, 1758	<i>Pinnixa faba</i> (Dana, 1851) [1] <i>Orthotheres haliotidis</i> n. sp.
<i>Haliotis coccoradiata</i> Reeve, 1846	<i>Pinnixa faba</i> (Dana, 1851) [1]
<i>Haliotis squamata</i> Reeve, 1846	<i>Orthotheres haliotidis</i> n. sp.
Acmaeidae	
<i>Acmaea</i> sp.	<i>Calyptraeotheres granti</i> (Glasell, 1933) [4]
<i>Acmaea mesoleuca</i> Menke, 1851	<i>Calyptraeotheres granti</i> (Glasell, 1933) [4]
Fissurellidae	
<i>Megathura granulata</i> (Sowerby, 1825)	<i>Fabia canfieldi</i> Rathbun, 1918 [6] <i>Opisthopus transversus</i> Rathbun, 1893
Trochidae	
<i>Cittarium pica</i> (Linnaeus, 1758)	<i>Orthotheres barbatus</i> (Desbonne, 1867) [3]
Turbinidae	
<i>Astraea undosa</i> (Wood, 1828)	<i>Opisthopus transversus</i> Rathbun, 1893
<i>Turbo</i> sp.	<i>Orthotheres barbatus</i> (Desbonne, 1867)
<i>Turbo argyrostomus</i> Linnaeus, 1758	<i>Orthotheres turboe</i> Sakai, 1969
<i>Turbo intercostalis</i> Menke, 1843	<i>Pinnotheres</i> sp.
Calyptraeidae	
<i>Calyptrea</i> sp.	<i>Pinnotheres politus</i> (Smith, 1870) [5]
<i>Crepidula</i> sp.	<i>Calyptraeotheres granti</i> (Glasell, 1933) [4]
<i>Crepidula dilatata</i> Lamarck, 1822	<i>Pinnotheres politus</i> (Smith, 1870) [5]
<i>Crepidula nivea</i> C. B. Adams, 1852	<i>Calyptraeotheres granti</i> (Glasell, 1933) [4]
<i>Crucibulum spinosum</i> (Sowerby, 1824)	<i>Calyptraeotheres granti</i> (Glasell, 1933) [4]
Strombidae	
<i>Strombus</i> sp.	<i>Orthotheres serrei</i> (Rathbun, 1909) <i>Orthotheres strombi</i> (Rathbun, 1905)
<i>Strombus alatus</i> Gmelin, 1791	<i>Orthotheres strombi</i> (Rathbun, 1905)
<i>Strombus pugilis</i> Linnaeus, 1758	<i>Orthotheres strombi</i> (Rathbun, 1905)
Naticidae	
<i>Polinices lewisi</i> (Gould, 1847)	<i>Opisthopus transversus</i> Rathbun, 1893
Muricidae	
<i>Coralliophaga</i> sp.	<i>Pinnotheres laevis</i> Bürger, 1895
Fasciolariidae	
<i>Pleuroploca</i> sp.	<i>Orthotheres strombi</i> (Rathbun, 1905)
Conidae	
<i>Conus</i> sp.	<i>Pinnotheres</i> sp.
<i>Conus pulcher</i> Lightfoot, 1886 [2]	<i>Ernestotheres conicola</i> (Mannig and Holthuis, 1981) [7]

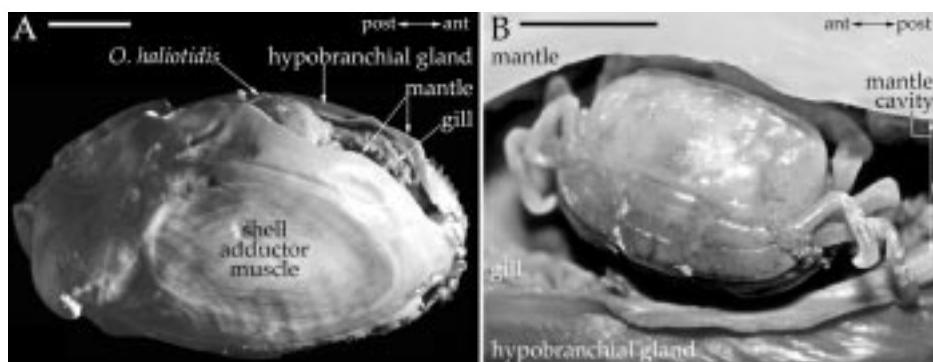


Figure 1. *Haliotis squamata* (BMNH 1907.12.9.257) with the shell removed showing *Orthotheres haliotidis* n. sp. (BMNH 1997.582) in situ. The label 'hypobranchial gland' points to the location of the gland, although the glandular tissue is situated towards the lumen of the mantle cavity. A: entire specimen with female crab, situated in anterior part of mantle cavity. Scale bar = 10 mm. B: enlarged view of female *O. haliotidis* n. sp. in mantle cavity of *H. squamata*. The cross hatching on the hypobranchial gland is due to the oblique orientation of the lamellae of this organ. Scale bar = 5 mm.

from the western Atlantic, and one (*O. unguifalcula*) from the eastern Pacific. Only *O. turboe* is found anywhere near Australia; it had been described from Yoron Island, Amani Group, Japan (Sakai, 1969). The species described earlier by Nakasone (1937: *fide* Sakai, 1969) based on material from "Palao Island" (= Palau = Belau) is also attributed to *O. turboe* (Sakai, 1969). In both instances *Turbo argyrostomus* Linnaeus, 1758—a widespread species in the Indo-Pacific (Abbot and Dance, 1983, Wilson, 1993)—was the host (Sakai, 1969).

MATERIALS AND METHODS

ABBREVIATIONS USED.—BMNH: The Natural History Museum, London; LACM: Los Angeles County Museum of Natural History.

The abalone were pried loose from their shells and the crabs were removed from the mantle cavity. For specimens catalogued LACM 79-54.3 and LACM 79-54.4, line drawings were made with a camera lucida attached to a Wild M5APO dissecting scope. All relevant appendages were removed from the bodies, rehydrated through an ethanol series to water containing very little detergent (1 drop per 28 ml), and sonicated for 15–30 s depending upon the fragility of the appendage. They were then transferred through an ethanol series to 100% ethanol, and then 100% Hexamethyldisilizane (Polysciences 00692) and air dried at NTP (see Nation, 1983). They were mounted on double-sided carbon adhesive (Ted Pella 16084-2) and/or colloidal graphite on a coin of 24 mm diameter. The coin was mounted on a Cambridge stub with colloidal graphite and sputter-coated with gold. The specimens were viewed at an accelerating voltage of 10 kv and a probe current of 200 pA on a Cambridge 360 Stereoscan scanning electron microscope (SEM) using the secondary electron detector. The resulting TIFF files were assembled to figures in Photoshop 3.05 (Adobe, 1994). The conspecific identity of BMNH 1997.582-583 to LACM 79-54.4 was assessed visually.

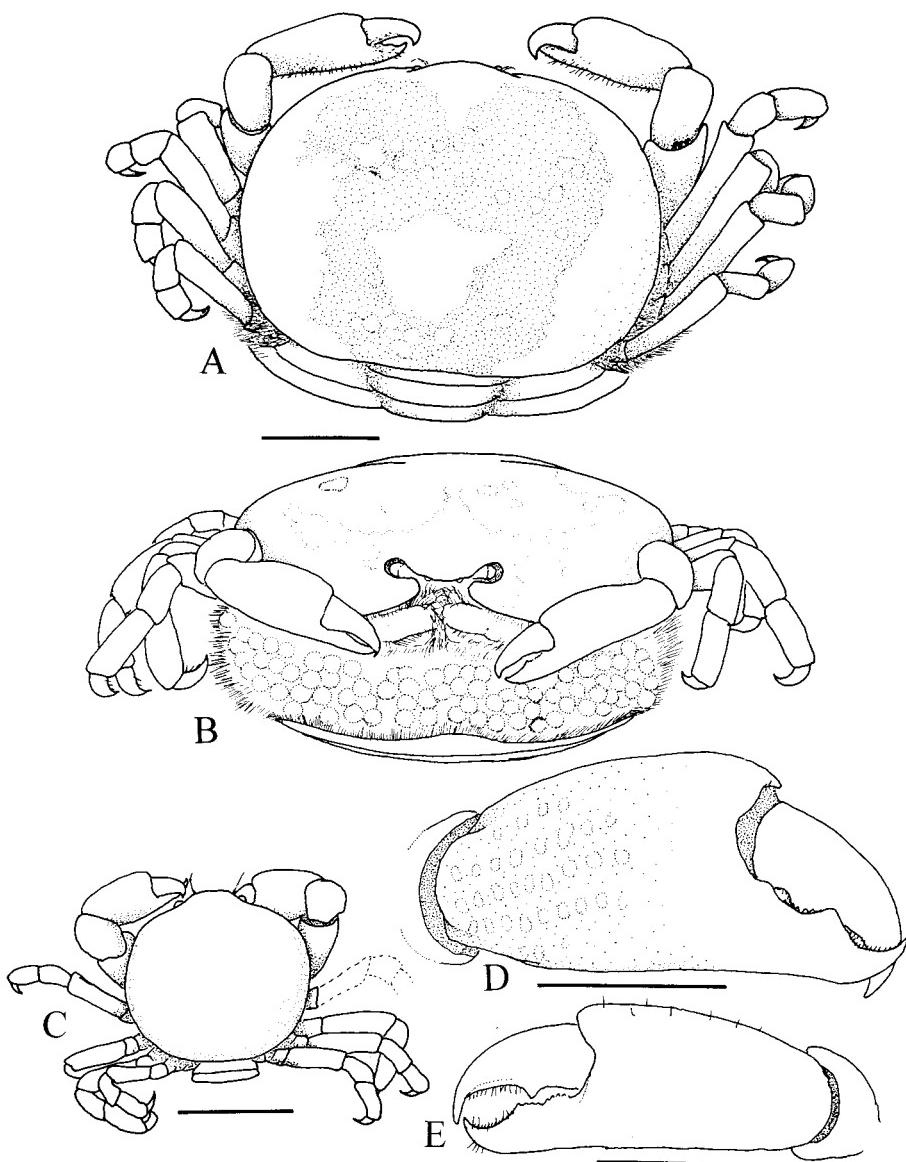


Figure 2. Camera lucida drawings of *Orthotheres haliotidis* n. sp. A, B: female holotype. Scale bar = 2.5 mm. A: dorsal. B: frontal. Note eggs between body and abdomen. C: male allotype dorsal. Scale bar = 2.5 mm. D: male allotype, exterior view of right claw. Scale bar = 1 mm. E: female holotype, exterior view of left claw. Scale bar = 1 mm.

SYSTEMATICS

Family *Pinnotheridae* de Haan, 1833

Genus *Orthotheres* Sakai, 1969

Type species, original designation: *Orthotheres turboe* SAKAI, 1969

Diagnosis —(modified from Campos (1989) to include the species described herein; modification indicated by underlining).—Carapace of the female appreciably broader than long, subrectangular, or transversely elliptical; the front is deflexed. Outer maxilliped obliquely placed, ischium indistinguishably fused with the merus; palpus three articles, inserted end to end, carpus longer than propodus and dactylus together or shorter than propodus (new species only), dactylus very small, about twice as long as wide, its length fits more than two times in the propodus. The anterior three pairs of walking legs generally subequal in length, the last pair always more slender and shorter than the preceding ones. The dactylus of all pairs is uniformly short and hooked at the tip.

Orthotheres haliotidis new species

Material Examined.—Holotype (Figs. 2A–B, 2E, 4C–D, 5C–D, 6B, 6D), ovigerous female, body in ethanol, third maxilliped, left claw, and second walking leg mounted on SEM stub, LACM 79-54.3; Allotype, male (Figs. 2C–D, 3, 4A–B, 4E, 5A–B, 6A, 6C, 7), body in ethanol, third maxilliped, left claw, second walking leg, and first pleopod (= gonopod) mounted on SEM stub, LACM 79-54.4; Host: *Haliotis asinina* LACM 79-54. Paratypes, male and ovigerous female (Fig. 1) in ethanol, BMNH 1997.582-583; Host: *Haliotis squamata* BMNH 1907.12.9.257 (Fig. 1).

Dimensions.—HOLOTYPE: carapace width (CW) 8.8 mm, carapace length (CL) 6.2 mm; ALLOTYPE: CW 3.7 mm, CL 3.8 mm. Host of holotype and allotype: shell length (SL) 48.3 mm. FEMALE PARATYPE: CW 9.6 mm, CL 7.0 mm. MALE PARATYPE: CW 3.6 mm, CL 3.7 mm. Host of paratypes: SL 62.0 mm.

Type locality.—Australia, Queensland, Lizard Island, between Lizard Head and Coconut Beach ($14^{\circ}40.9'S$, $145^{\circ}28.0'E$); leg. J. H. McLean, 5 June 1979.

Additional locality.—Australia, Western Australia, Freemantle; leg. G. B. Sowerby III, 1901, BMNH 1997.582.583.

Etymology.—Referring to the reported host genus *Haliotis* (Mollusca, Gastropoda, Vetigastropoda, Haliotidae), i-declension, femininum, genitive singular, as a patronym.

Carapace.—In female (Fig. 2 A-B) much wider than long, strongly convex, smooth, rostrum not extending beyond level of eyes; in male (Fig. 2C) length and width nearly even, or slightly longer than wide, rostrum extending slightly beyond level of eyes.

Third maxillipeds (Figs. 3 A, 4).—Dactylus minute, long, and thin, nearly three times longer than wide, with five to seven setae confined to tip of article. Dactylus inserted at tip of propodus. Propodus longer than wide, with small protuberance extending dorsally and distally over insertion point of dactylus and reaching to about half length of dactylus. Propodus longer than dactylus or carpus. Dorsal surface of propodus with dense covering of serrate setae. Carpus short, stout, with thick covering of serrate and plumose setae. Merus and ischium fused, broad, nearly rectangular, with scattered setae on external surface and plumodenticulate setae along lateral border.

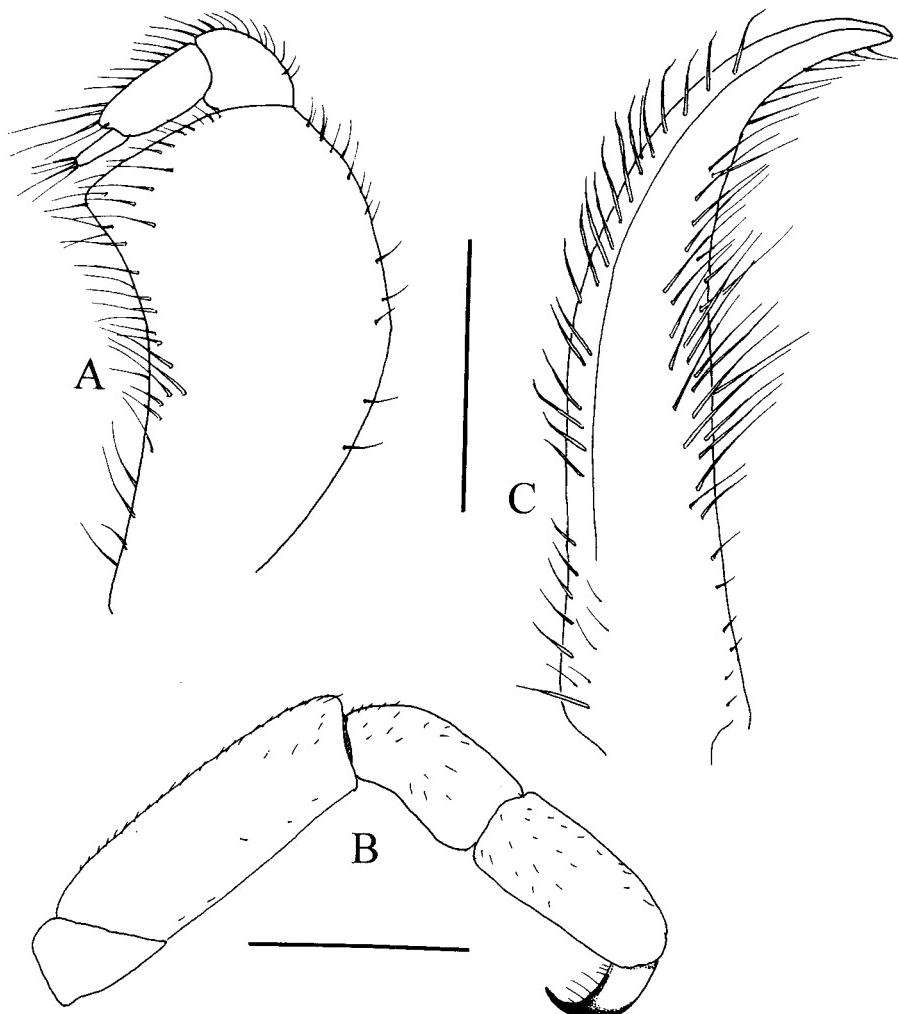


Figure 3. Camera lucida drawings of *Orthotheres haliotidis* n. sp.: appendages of male allotype (LACM 79-54.4). A: third maxilliped. Scale bar = 0.5 mm. B: walking leg. Scale bar = 1 mm. C: gonopod. Scale bar = 0.5 mm.

Chelipeds (Fig. 5).—Robust, well developed, that of male (Fig. 5A–B) thicker and higher than that of female (Fig. 5C–D). Tips of fingers acute, overlapping when closed. Movable finger (dactylus) with strong tooth at proximal one quarter of length, with tip of tooth fitting into shallow groove in propodal finger. Immovable finger (propodus) with short, triangular tooth at midlength, followed proximally by smaller teeth giving a serrate appearance. Distal half of both fingers with row of sharp, short spines, and more widely spaced setae. Inner surface of propodus with field of setae spreading from tip back onto inner surface of palm; inner surface of dactylus with fewer, smaller setae.

Walking legs (Fig. 6).—All walking legs with dactylus short, less than half length of propodus, strongly recurved distally. Inner surface of dactylus bearing three or four minutely plumodenticulate setae (those of male in Figs. 6A, 6C bear debris).

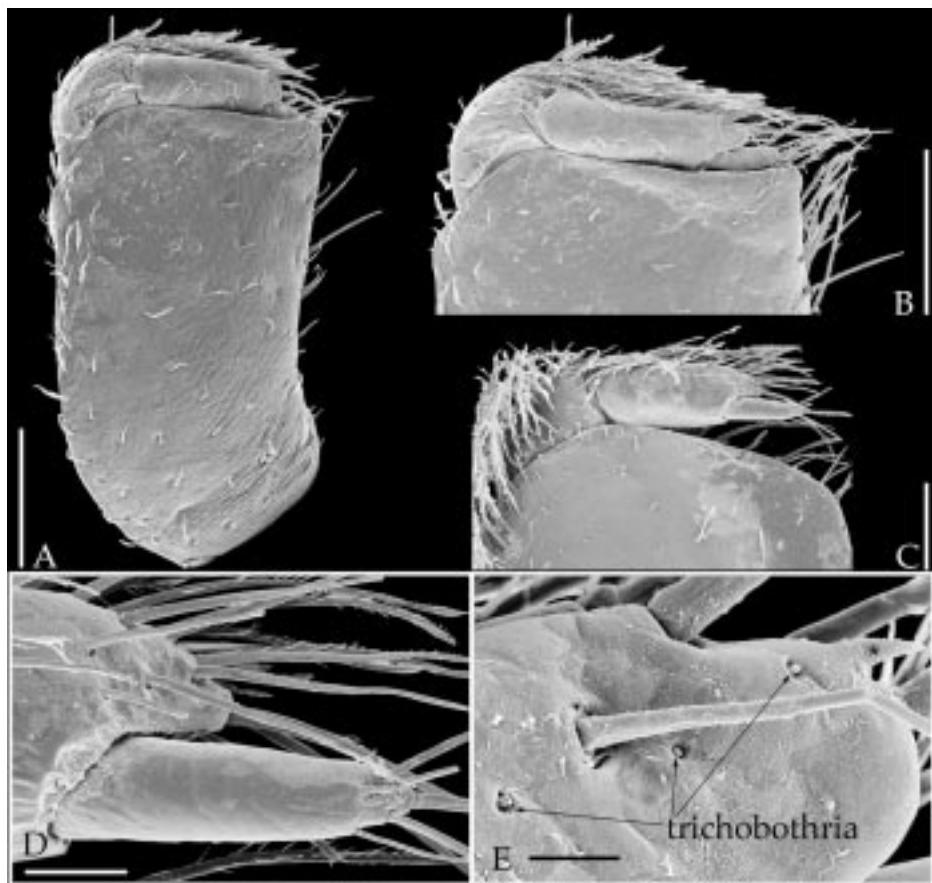


Figure 4. Third maxilliped of *Orthotheres haliotidis* n. sp. A: entire maxilliped, male allotype (LACM 00000). Scale bar = 200 μm . B: terminal portion of A enlarged. Scale bar = 200 μm . C: terminal portion enlarged, female holotype (LACM 79-54.3). Scale bar = 200 μm . D: dactylus of C enlarged. Scale bar = 50 μm . E: upper, terminal of propodus, enlarged from B. Note trichobothria and terminal spine (*). Scale bar = 10 μm .

Male first pleopods (gonopods) (Fig. 7).—Large, longer than the third maxillipeds, distal third strongly curved laterally and tapering to a blunt tip directed almost 90° from shaft of pleopod. Medial and lateral borders bearing long, unarmed setae especially on distal half.

Hosts.—The only hosts known are *Haliotis asinina* and *H. squamata*. Most likely, *O. haliotidis* occurs also in *H. coccoradiata* where it is mentioned as *Pinnixa faba* in earlier reports.

Remarks.—The following characters clearly place our species in the genus *Orthotheres*: the minute dactylus of the third maxilliped (Figs. 3A, 4), the manner in which it is inserted “at the end” on the tip of the propodus, the short and strongly curved dactyli on all walking legs, and the fact that the fifth walking leg is similar to the others but slightly smaller. However, the generic character “carpus [of third maxilliped] longer than propodus and dactylus together” given by Campos (1989: 1123) does not apply, as in our species the propodus is relatively large, and clearly exceeds the length of the carpus, such that the combined dactylus-propodus length is nearly twice the length of the carpus (see Fig. 3B).

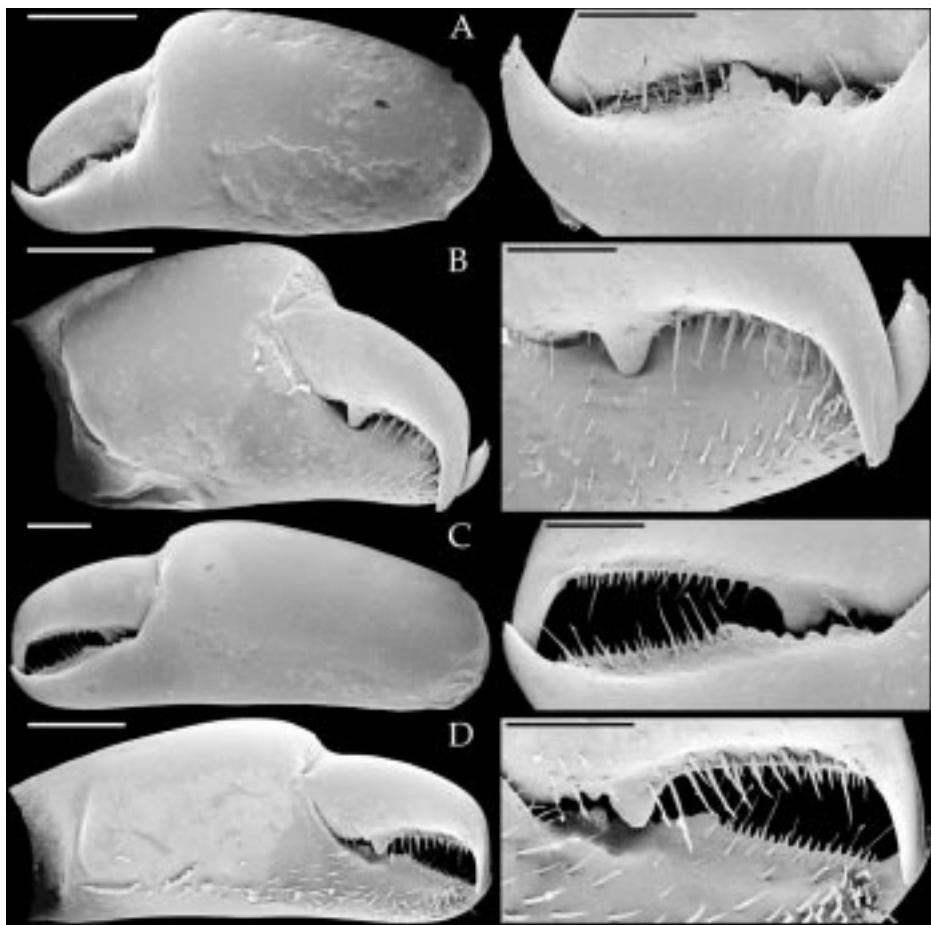


Figure 5. Claws of *Orthotheres haliotidis* n. sp.: on left, the entire claw is shown; on right enlarged cutting surface of claw. SEM. A-B allotype LACM 79-54.4. Scale bar entire claw = 500 μ m. Scale bar cutting surface = 200 μ m. B-C female holotype LACM 79-54.3. Scale bar entire claw = 500 μ m. Scale bar cutting surface = 250 μ m. A: Exterior view of male claw. B: Interior view of male claw. C: Exterior view of female claw; ridges in ventral portion of base is an artifact consisting of colloidal graphite. D: Internal view of female claw.

In lieu of erecting a new genus for *O. haliotidis*, we have modified the generic diagnosis of *Orthotheres* to accommodate it.

Although previous descriptions of *Orthotheres* spp. have not employed SEM or included detailed descriptions of some of the taxonomically important characters, *O. haliotidis* clearly does not conform to any of the existing descriptions of *Orthotheres* spp. The form of the dactylus and the propodus of the third maxilliped (Figs. 3A,4) differs markedly from that of the eastern Pacific *O. unguifalcula*, wherein these articles together form a stout and almost triangular projection from the carpus in that species (see Campos, 1989: fig. 3a).

The western Pacific species, *O. turboe*, is similar to *O. haliotidis*, and Sakai's figure (Sakai, 1969: fig. 19a) of the third maxilliped dactylus agrees closely with our figure for *O. haliotidis*. However, the carpus of this appendage in *O. turboe* is large, whereas in *O. haliotidis* the propodus exceeds the length of the carpus (Fig. 3A) as noted earlier. Ernesto

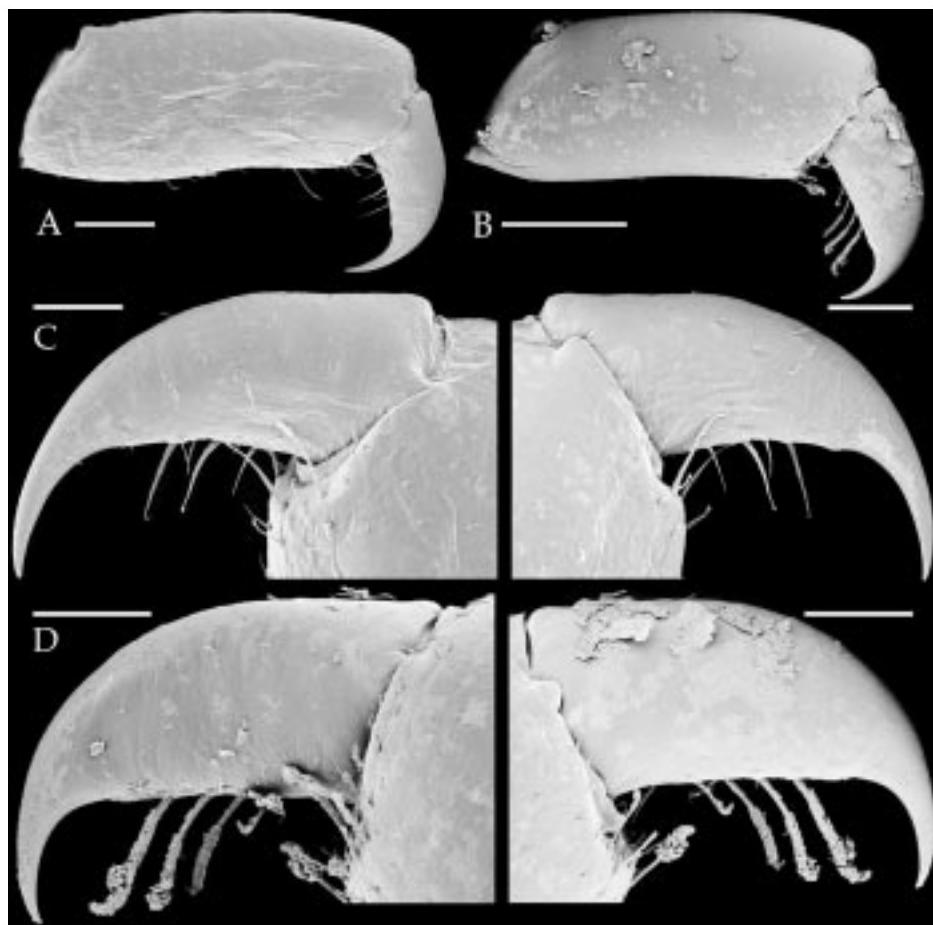


Figure 6. Second walking leg of *Orthotheres haliotidis* n. sp. A-B. Propodus and dactylus. A: male allotype (LACM 79-54.4). Setae are bearing debris. Scale bar = 200 µm. B: female holotype (LACM 79-54.3). Scale bar = 500 µm. C-D: dactylus. Left: internal view. Right: exterior view. C: male allotype. Setae bear debris. Scale bar = 100 µm. D: female holotype. Scale bar = 200 µm.

Campos (pers. comm.) has suggested that this difference plus the slightly subterminal insertion of the dactylus might argue for erection of a new genus. Additionally, in *O. turboe*, Sakai described the movable finger of the chela as "unarmed," which is not the case in *O. haliotidis* (Figs. 2D-E,5). Sakai (1969: 277) undoubtedly meant the immovable finger, rather than movable, as his preceding sentence described the "dactylus armed with a tooth near the proximal end of the prehensile edge," and the dactylus is of course the movable finger. Even if Sakai was referring to the immovable finger (the extension of the propodus) as being unarmed, it is nevertheless a distinct difference from the chela of *O. haliotidis*, in which both fingers are well armed (Figs. 2D-E,5).

Of the three western Atlantic species (*O. barbatus*, *O. serrei*, and *O. strombi*), Rathbun's (1918: all as *Pinnotheres*) monograph allows rather easy differentiation. For *O. barbatus*, both Rathbun (1918) and Gore (1986) described the male as having pubescence covering the chela, and with dense setation on the undersurface and on all legs, a condition not at all similar to the new species (Figs. 2D-E,5). In *O. serrei*, Rathbun (1918) described the

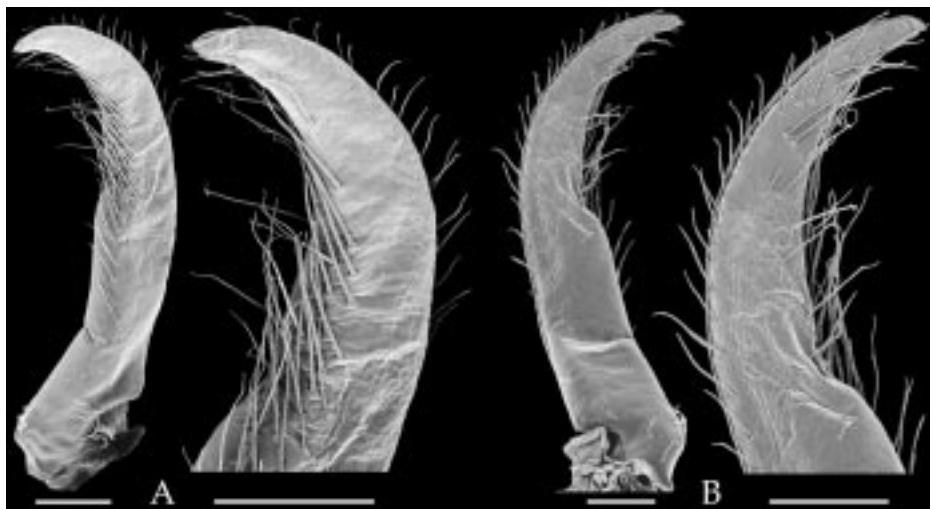


Figure 7. Gonopod of *Orthotheres haliotidis* n. sp.: male allotype LACM 79-54.4. SEM. A: Anterior view. B: Posterior view. On left, entire gonopod; on right, tip enlarged. Scale bar = 200 μ m.

male as being “spotted all over” and having a cristate sternum, and the female as having the “merus of the first three legs fringed with long hairs,” among other salient differences. In *O. strombi*, Rathbun described the maxillipedal carpus as being short and stout, and her illustration (Rathbun, 1918: fig. 45) highlights this difference between *O. strombi* and the new species. Thus, all five species previously included in *Orthotheres* can be readily separated from *O. haliotidis*.

DISCUSSION

Typically only single specimens of pea crab are found in each host. However, species in the genus *Orthotheres* have been reported to occur usually in pairs (Sakai, 1969), as in the two cases reported here. Although some Australian abalone species are of commercial importance (*H. rubra* Leach, 1814, *H. laevigata* Donovan, 1808), neither of the hosts reported are. This situation explains the spotty record of pinnotherid crabs in abalone. During related work, DLG has inspected at least 50 preserved specimens of *H. asinina*, a dozen *H. squamata*, and many more specimens from the Australian region, but only the two symbiont containing specimens were discovered. The frequency of the association reported here must be termed at most uncommon.

The distribution of the hosts is as follows. *H. asinina* is a wide-spread species in the tropical Pacific. It ranges from the Andamans to Singapore, Vietnam, Okinawa, South Honshu, Guam, Solomon Islands, Fiji, New Caledonia, North of Sydney (New South Wales), North of Shark Bay (Western Australia), and Indonesia. *H. squamata* ranges from Perth, Western Australia, northwards to central Northern Territories with some isolated records in Indonesia, Andamans and Vietnam (Geiger, unpubl.).

The location of the pinnotherid symbiont within the gastropod host has been described as being the “stomach” (Sakai, 1969, Campos, 1989). We argue that this indication is an error in terminology and should read “mantle cavity.” First, all pinnotherids in mollusks have been reported from the mantle cavity, and second, the hosts (*Turbo*, *Strombus*) re-

ported by the above authors are herbivores and detritivores (Purchon, 1968, Götting, 1974, Walls, 1980), as are all species of *Haliotis* (e.g., Crofts, 1929, Cox, 1962, Shepherd, 1973). Feeding on pea crabs would be extremely difficult for these species, which would be physically unable to swallow them whole. In both association observed by us, the female specimen was situated in the posterior part of the mantle cavity, whereas the male was located close to the anterior end, i.e., where relatively fine, left outer membrane of the mantle ends (Fig. 1).

Pea crabs are on the dividing line between commensals and parasites, sometimes referred to as semiparasites, as they can cause damage to the gill tissue of the molluscan host (Jones, 1978 for discussion). We could not see any such damage on the gill, the hypobranchial gland, the rectum, or the mantle, as shown by comparison to symbiont-free hosts (see Fig. 1). The presence of a symbiont is only evidenced by some limited pitted marks in the ventral portion, or floor, of the mantle cavity. The dactyli of some walking legs were situated in these pits when the abalone was dislodged from its shell.

ACKNOWLEDGMENTS

K. Way accommodated D.L.G. during the stay at the BMNH and made the loan of a specimen possible. SEM time was paid by NSF Grant DEB 9020088 to J.W.M. R. Mannig and E. Campos kindly discussed and confirmed our initial conclusions. F. M. Bayer helped determine the correct construction of the species name. Two anonymous reviewers improved this manuscript.

LITERATURE CITED

- Abbott, R. T. and S. P. Dance. 1983. Compendium of seashells. 2nd printing (rev.). E. P. Dutton, Inc., New York. xi + 411 p.
- Adobe. 1994. Adobe Photoshop 3.05. Adobe Systems Incorporated, Mountain View, California.
- Allen, J. 1959. Australian shells. Charles T. Brandford Company, Boston. 487 p.
- Bhavanarayana, P. V. and S. L. Devi. 1974. On the frequency of occurrence of *Pinnotheres* sp. in the window-pane oyster, *Placenta placenta* (Linné). Current Sci. 43: 255–256.
- Bernard, P. A. 1984. Shells of Gabon. Bernard, Libreville. 140 p.
- Campos, E. 1989. Comments on the taxonomy of the genus *Orthotheres* Sakai, 1969 (Crustacea, Brachyura, Pinnotheridae). Bull. Mar. Sci. 44: 1123–1128.
- _____. 1990. *Calyptraeotheres*, a new genus of Pinnotheridae for the limpet crab *Fabia granti* Glassell, 1933 (Crustacea, Brachyura). Proc. Biol. Soc. Wash. 103: 364–371.
- _____. 1993. Systematics and taxonomic remarks on *Pinnotheres muliniarum* Rathbun, 1918 (Crustacea: Brachyura: Pinnotheridae). Proc. Biol. Soc. Wash. 106: 92–101.
- Chace, F. A. Jr. and D. P. Abbott. 1980. Chapt. 23 Caridea: The shrimps. Pages 567–576 in R. H. Morris, D. P. Abbott, and E. C. Haderlie. Intertidal invertebrates of California. Stanford Univ. Press, Stanford, California.
- Crofts, D. R. 1929. *Haliotis*. Liverpool marine biology committee memoirs vol. 29:1–174, 8 pls.
- Cox, K. W. 1962. California abalones, family Haliotidae. Fish. Bull., U.S. 118: 1–131.
- Fischer, P.-H. 1976. Remarques sur *Haliotis asinina* L. [Remarks on *Haliotis asinina* L.]. J. Conchyl. 113: 53–54.
- _____. and E. Fischer-Piette. 1976. *Gastrarium pectinatum* L. hôte d'un pinnotère [*Gastrarium pectinatum* L. host of a pinnotherid]. J. Conchyl. 113: 87.
- Gore, R. H. 1986. *Fabia felderii* species novum, a new pinnotherid crab from the central eastern coast of Florida (Crustacea: Decapoda: Brachyura). Northeast Gulf Sci. 8: 143–148.
- Götting, K.-J. 1974. Malakozoologie [Malacozoology]. Gustav Fischer Verlag, Stuttgart. 320 p.

- Grant, F. E. and A. R. McCulloch 1906. On a collection from Port Curtis District, Queensland. Proc. Linn. Soc. New South Wales 31: 2–53.
- Haswell, W. A. 1882. Catalogue of the Australian stalk- and sessile-eyed Crustacea. The Australian Museum, Sydney. 324 p., 4 pls.
- Jensen, G. C. 1995. Pacific coast crabs and shrimps. Sea Challengers, Monterey. 87 p.
- Jones, J. B. 1978. Natural history of the pea crab in Wellington Harbour, New Zealand. N. Z. J. Mar. Freshw. Res. 11: 667–676.
- Konishi, K. 1977. On three species of the pinnotherid crabs from Hokkaido, Japan. J. Fac. Sci. Hokkaido Univ. Ser. 6 Zool. 20: 605–610, pl. 21.
- Korkos, D. and B. S. Singer. 1995. A “pea” crab in *Glycymeris pectunculus*. Levantina 82: 14.
- Manning, R. B. 1993. West African pinnotherid crabs, subfamily Pinnotherinae (Crustacea, Decapoda, Brachyura). Bull. Mus. Nat'l. Hist. Nat., Paris, ser. 4, sect. A, 15: 125–177.
- _____, and L. B. Holthuis. 1981. West African brachyuran crabs (Crustacea: Decapoda). Smithsonian Contrib. Zool. 306: xii, 1–379.
- Nation, J. L. 1983. A new method using hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. Stain Technol. 38: 347–351.
- Purchon, R. D. 1968. The Biology of the Mollusca. Pergamon Press, Oxford. 560 p.
- Rathbun, M. J. 1918. The grapsoid crabs of America. U.S. Natl. Mus. Bull. 97: 1–461.
- Sakai, T. 1969. Two new genera and twenty-two new species of crabs from Japan. Proc. Biol. Soc. Wash. 82: 243–280.
- Schmitt, W. L., J. C. McCain and E. S. Davidson. 1973. Decapoda I. Brachyura I. Fam. Pinnotheridae. Pages 1–160 in H.-E. Gruner and L. B. Holthuis. Crustaceorum Catalogus Pars 3. Dr. W. Junk B. V., Den Haag.
- Schneider, J. A. 1993. The crab, *Pinnixa faba* (Pinnotheridae), in the bivalve, *Clinocardium (Keenocardium) californiense* (Cardiidae). Bull. Mar. Sci. 52: 842–843.
- Shepherd, S. A. 1973. Studies on southern Australian abalones. 1: Ecology of five sympatric species. Austr. J. Mar. Freshw. Res. 24: 217–257.
- Stevens, P. M. 1992. New host record for pea crabs (*Pinnotheres* spp.) symbiotic with bivalve molluscs in New Zealand (Decapoda, Brachyura). Crustaceana 63: 216–220.
- Walls, J. G. 1980. Conchs, Tibias, and Harps. T. F. H., Neptune, New Jersey. 191 p.
- Wilson, B. 1993. Australian marine shells. vol. 1. Odyssey Publishing, Kallaroo. 408 p.
- Zmarzly, D. L. 1992. Taxonomic review of the pea crabs in the genus *Pinnixa* (Decapoda: Brachyura: Pinnotheridae) occurring on the California shelf, with description of two new species. J. Crustacean Biol. 12: 677–713.

DATE SUBMITTED: September 8, 1997. DATE ACCEPTED: 8 December 1997.

ADDRESSES: (D.L.G.) Department of Biological Sciences, University of Southern California, Los Angeles, California 90089-0371, e-mail dgeiger@scf.usc.edu. (J.W.M) Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007, e-mail: jmartin@bcf.usc.edu.